HERITABLE LIFE HISTORY VARIATION IN WIDELY SEPARATED POPULATIONS OF *MESOCYCLOPS EDAX* (CRUSTACEA: COPEPODA)

GRACE A. WYNGAARD

Department of Zoology, University of Maryland, College Park, Maryland 20742

ABSTRACT

Additive genetic variances were estimated for several life history traits of north temperate Michigan and subtropical Florida populations of the freshwater copepod *Mesocyclops edax* (Crustacea: Copepoda). Estimates were obtained by rearing animals at 25°C and using a paternal half sib design. Considerable additive genetic variance was revealed in female and male body sizes of the Florida population and in female and male maturation times in the Michigan population. Female maturation time and clutch size in the Florida population and female body size and clutch size in the Michigan population exhibited low additive genetic variance. These findings provide further evidence of substantial additive genetic variance in life history traits of natural populations. The contrasting trends in additive genetic variance underlying life history traits of these populations are interpreted as reflecting differences in the potential to respond to selection and possibly also the different selective regimes of the Michigan and Florida environments.

INTRODUCTION

The variation in many life history traits of interest to evolutionary biologists is polygenic (Istock, 1981; Dingle and Hegmann, 1982; Lande, 1982) and suitable for quantitative genetic analyses. Plant and animal breeders have used such analyses to partition phenotypic variation into genetic and environmental components, and thus to predict responses to selection. Much experimental work on domesticated animals and plants, and on laboratory *Drosophila* populations, has documented changes in the proportion of additive genetic variance relative to other sources of variation after selection has been applied (see Falconer, 1980, for review). Often these findings bear out the predictions of Fishers' Fundamental Theorem of Natural Selection (Fisher, 1958): that traits exhibiting low additive genetic variance and thus showing low heritability (ratio of additive genetic variance to total phenotypic variance) are presumed to have had much of their additive genetic variance trimmed away by directional selection. It is not known, however, whether this principle can be generally applied to natural populations.

Some recent studies have uncovered substantial heritable variation in life history traits in natural populations and have attributed this variation to frequent changes in direction of selection (Dingle *et al.*, 1977; Istock, 1981) or to weak selection and negative pleiotropy (Berven and Gill, 1983). As a population's potential response to selection is, in theory, proportional to the heritable variation in fitness, the additive genetic variances of fitness characters are of interest when investigating life history evolution. If adaptation to a new environment results in changes in the amounts of additive genetic variance of particular traits, then changes in additive genetic variance

might be useful for inferring shifts in the relative contributions of traits to fitness. This line of reasoning was first applied to heritability analyses of a marine copepod by McLaren (1976) and of an estuarine copepod by Bradley (1978). Few organisms evolve rapidly in nature to provide an opportunity to observe such changes in additive genetic variance. An alternative is to examine geographically isolated populations of the same species that have presumably undergone evolution and genetic differentiation in response to their separate environments. This comparative approach attempts to provide insight into why specific traits might exhibit high additive genetic variance in one population and low additive genetic variance in another.

In this study I estimate the additive genetic variances underlying phenotypic variation in several life history traits in two populations of *Mesocyclops edax* (S. A. Forbes) (Crustacea:Copepoda) from different locales. The two environments differ in several obvious ways: trophic status, thermal regime, and predator abundance and diversity. These populations show genetically based differences in the means of several traits (Wyngaard, 1986). Individuals from Florida exhibit more rapid maturation rates, larger body sizes, and larger clutch sizes than do those from Michigan. These traits are known to influence either survival and fecundity in natural zooplankton populations (Allan, 1976; Lynch, 1980; Kerfoot, 1980) and thus may be viewed as important fitness components. These two populations show no reproductive barriers in the laboratory, have fertile hybrids (Allan, 1984), and thus seem to be conspecific. The genetic differentiation in life history traits between the populations leads one to ask whether there have also been changes in the heritable variation of these traits. The purpose of this study was to estimate and compare the additive genetic variances of several fitness components among two geographically distinct copepod populations and to explore the usefulness of this information in making inferences regarding the potential to respond to selection as well as the past selective regimes experienced by these populations.

MATERIALS AND METHODS

Field study sites

Individuals of *Mesocyclops edax* were collected from Lake Thonotosassa, Hillsborough County, Florida, on 10 July 1981 and from Douglas Lake, Cheyboygan County, Michigan, on 23–26 June 1981. Detailed descriptions of Lake Thonotosassa are given by Cowell *et al.* (1975) and Wyngaard *et al.* (1982) and descriptions of Douglas Lake are provided by Welch (1927), Tucker (1957), and Lind (1978). Here the Lake Thonotosassa population is designated as FT and the Douglas Lake population as MD. Plankton were shipped by air to the laboratory within 24 h of collection.

Experimental design

Additive genetic variance components and narrow sense heritabilities were estimated with a paternal half sib mating design (*e.g.,* Falconer, 1980), using laboratory-reared animals that had undergone one generation of laboratory acclimation. Haphazardly sampled adult males and juvenile females from each population in nature were isolated in pairs and mated to yield the acclimation generation (G_1). Sixty-nine MD (Douglas Lake, Michigan) and sixty-six FT (Lake Thonotosassa, Florida) matings were successful; four to twenty progeny from each of these matings were reared to adulthood. The adults of this acclimation generation were mated using a paternal half sib mating design in which two females (dams) were mated to a single male (sire). No adult was related to any other adult in the mating scheme. A total of 14 MD and 15 FT half sib families were obtained. Twenty offspring from each dam were reared to

maturity and mated, taking care to mate only unrelated individuals. These offspring comprised the second generation (G_2) on which the additive genetic variances of the life history traits were estimated.

No acclimation effects in maturation rate, body size (cephalothorax length), and clutch size were revealed between the two generations reared in the laboratory as mean values of these traits did not differ significantly (Wyngaard, 1983). Survival from hatching to adulthood of G_1 individuals in both populations was 97%. Survival of G_2 individuals of FT and MD populations was 96% and 91%, respectively.

Laboratory rearing

Upon hatching, progeny were replaced individually in petri dishes 20 mm deep and 60 mm in diameter containing artificial lake water (Wyngaard and Chinnappa, 1982) and 10^4 cells/ml of *Cryptomonas ozolini* Skÿjja (Starr Collection UTEX LB2194) isolated from Douglas Lake. The adult diet of *M. edax* was supplemented with the calanoid *Diaptomus dorsalis* (a common prey of *M. edax* in Lake Thonotosassa). *D. dorsalis* was mass cultured on *Chylamydomonas reinhardti* (Starr Collection No. 89) and artificial lake water. Algae and crustaceans were grown at $25 \pm 0.5°C$ and a light:dark cycle of 14:10. Individual *M. edax* were transferred to clean dishes with fresh medium and food every other day, and individuals were observed daily for survival and development. Upon maturity, unrelated males were placed with females until the first clutch was produced. Animals were preserved in 4% formaldehyde for body size and clutch size measurements. Cephalothorax length was measured to the nearest 0.003 mm at 40× with an ocular micrometer.

Calculations of additive genetic variance components

The sire variance component estimates the phenotypic covariance of half sibs and thus estimates one fourth of the additive genetic variance, because half sibs have one fourth of their genes in common, on the average (Falconer, 1980). Estimates from half sibs provide the best unbiased estimate of additive genetic variance. Dam component estimates, which include variance due to dominance (non-additive), maternal effects, and common environment, in addition to the phenotypic covariance of half sibs, were calculated for comparison with the half sib estimates. Because individuals were reared individually after hatching, common family environment is not likely to be important. Upon reaching maturity, males and females were paired; the males were removed when the females produced eggs. Cannibalism of males by females after mating occurred occasionally in the FT matings and frequently in the MD matings, resulting in reduced numbers of males available for body size measurement. Sample size was too small to estimate the additive genetic variance of MD male body size. To minimize predation, some females and males were not mated but, instead, were preserved upon reaching maturity.

As is commonly the case in such studies, class sizes were unequal; this resulted from variation in sex ratio and (to a small degree) differential survival of offspring. All data were used, and variance components for additive genetic variances were computed using maximum likelihood estimation (MLE) procedure VARCOMP of the computer package SAS (Hemmerle and Hartley, 1973; Helwig and Council, 1979). This method of extracting parameter estimates differs from that used in ANOVA but assumes the same underlying genetic model. MLE is preferable to ANOVA, because unlike ANOVA, MLE does not result in negative variance components, which are unrealistic. The superiority of MLE to ANOVA for use on unbalanced data is discussed

by Swallow and Monahan (1984). Standard errors of additive genetic variance components of half sibs were estimated according to Searle (1970). The significance levels of sire effects (or additive genetic variances) were tested by comparing the objective functions of the MLE analyses when the sire effects were estimated separately from the dam and within family variances to when they were combined with the dam variances. These objective functions closely approximate the mean squares (Hemmerele and Hartley, 1973), and their difference yields a Chi square value (χ^2) which can be used to determine significance levels using 2 d.f. I present and compare estimates of additive genetic variance (V_A) in preference to heritability estimates (h^2), which are a ratio of the additive genetic variance (V_A) to the phenotypic variance (V_P). It is the genetic variance that is of interest in the present study; comparisons of V_A are not complicated by the problems of comparing ratios. One trait, maturation time, was transformed to natural logarithms.

RESULTS

The half sib (sire) components of variance on which the heritability analyses were based will be discussed first, as they provide the least biased estimates of additive genetic variance, and full sib (dam) components of variance will be discussed later. Neither population showed any significant heritable variation of clutch size or male maturation time (Tables I, III). There was a significant heritable variation for female maturation time in the MD population, but not in the FT population (Table I). In

TABLE I

Estimates of maximum likelihood variance components of maturation time (days) of Mesocyclops edax *from Lake Thonotosassa, Florida (FT) and Douglas Lake, Michigan (MD).*
Maturation time was transformed to natural logarithms

Population	Sex of offspring	Source of variation	d.f.	Variance component	(SE)	Percent of total variation	χ^2
FT	Female	Among sires	13	0.0	(0.001)	0.0	0
		Between dams, within sires	14	0.0050		39.1	
		Within families	204	0.0079		60.9	
		Total	231	0.0129		100.0	
MD	Female	Among sires	13	0.0163	(0.0077)	42.8	17.46***
		Between dams, within sires	14	0.0055		14.5	
		Within families	220	0.0162		42.7	
		Total	247	0.0381		100.0	
FT	Male	Among sires	13	0.0	(0.002)	0.0	0.01
		Between dams, within sires	14	0.0077		44.6	
		Within families	231	0.0096		55.4	
		Total	258	0.0173		100.0	
MD	Male	Among sires	10	0.0103	(0.010)	28.0	2.81
		Between dams, within sires	11	0.0178		48.3	
		Within families	117	0.0087		23.6	
		Total	138	0.0368		100.0	

*** $P < 0.001$.

contrast, there was significant heritable variation for female body size in the FT population but not in the MD population (Table II). The additive genetic variances of male body size could not be compared, because sample size was too small to obtain an estimate for the MD population (Table II).

The degree to which the variance component among full sibs exceeds that from the half sibs indicates, in theory, the contribution of maternal common environment and non-additive genetic dominance effects to the observed variation. Comparison of estimates based upon sire and dam components indicated considerable nonadditive genetic and/or maternal components for FT male and female maturation time MD male maturation rate (Table I) and clutch size (Table III). The only instance in which the sire and dam compounds approximated one another was for MD female body size. Three traits exhibited a dam variance considerably less than that of the sire variance: MD female maturation time and FT male and female body size.

DISCUSSION

The Florida (FT) population exhibited considerable additive genetic variance in body size, but not maturation time while the Michigan (MD) population showed the opposite trend. Both populations exhibited low additive genetic variance for clutch size. The standard errors of these variance components were large. However, in all cases (except maturation time of MD males) statistical tests of objective functions showed heritable variation only for traits that exhibited high amounts of additive genetic variance. Maturation time, body size, and clutch size influence survival and fecundity in natural populations and can be used to estimate the additive genetic variance of fitness components.

Before I discuss these genetic variance estimates, their limitations should be noted. Presumably these laboratory derived estimates of additive genetic variance reflect those

TABLE II

Estimates of maximum likelihood variance components of body size (μm) of Mesocyclops edax *from Lake Thonotosassa, Florida (FT) and Douglas Lake, Michigan (MD)*

Population	Sex of offspring	Source of variation	d.f.	Variance component	(SE)	Percent of total variation	χ^2
FT	Female	Among sires	14	31495	(4472)	13.7	9.09*
		Between dams, within sires	15	10409		4.5	
		Within families	160	187377		81.7	
		Total	189	229281		100.0	
MD	Female	Among sires	13	12210	(4472)	4.8	0.97
		Between dams, within sires	14	10906		4.8	
		Within families	174	231608		90.9	
		Total	201	254742		100.0	
FT	Male	Among sires	12	5849	(1348)	9.6	6.74*
		Between dams, within sires	13	0		0.0	
		Within families	125	54892		90.4	
		Total	150	60741		100.0	

* $P < .05$

TABLE III

Estimates of maximum likelihood variance components of clutch size of Mesocyclops edax *from Lake Thonotosassa, Florida (FT) and Douglas Lake, Michigan (MD).*

Population	Sex of offspring	Source of variation	d.f.	Variance component	(SE)	Percent of total variation	χ^2
FT	Female	Among sires	13	1.54	(3.75)	4.1	0
		Between dams, within sires	14	10.00		26.4	
		Within families	134	26.25		69.4	
		Total	161	37.78		100.0	
MD	Female	Among sires	10	0.00	(3.54)	0.0	0
		Between dams, within sires	11	5.58		24.3	
		Within families	74	17.44		75.7	
		Total	95	23.02		100.0	

of these populations in nature. The Florida population matures and reproduces over a wide temperature range (12–31°C) in nature, whereas the greater proportion of maturation and reproduction in the Michigan population occurs between 18–26°C. The lack of genotype-environment interactions, which would alter the additive genetic variances, is impossible to verify without repeating these experiments over a wide range of environmental conditions. Genotype-environment interactions have been reported for some life history traits in the marine copepod *Eurytemora herdmani* (McLaren, 1976) as well as for *Drosophila melanogaster* (Giesel *et al.,* 1980, but see Rose, 1984), but were absent for some traits in *D. pseudoobscura* (Tantawy, 1961). General remarks regarding the relevance of genotype-environment interaction to heritability studies are difficult to make, except that they can alter the interpretation of results and that they merit more investigation.

The observation of traits exhibiting high additive genetic variance in one population and low additive genetic variance in another is intriguing in itself. The mean values of these traits (maturation time, body size, clutch size) show genetically based differences between populations (Wyngaard, 1986). The two populations interbreed readily in the laboratory (Allan, 1984); thus these populations comprise one species and comparisons of their additive genetic variances are appropriate.

The trends in additive genetic variances reported in the present study may be meaningful in one or several regards. First, the amount of additive genetic variance of a trait may reflect the intensity of selection in the immediate past upon that trait. Fisher's Fundamental Theorem, which states that the rate of increase of mean population fitness at any time is proportional to the additive genetic variance in fitness (Fisher, 1958), provides a context in which the relative amounts of additive genetic variance estimated for traits in this study can be compared and discussed. Certainly the large standard errors around these estimates of additive genetic variance make comparisons between populations tenuous; however, the differences between populations in statistically detectable levels of additive genetic variance suggest such comparisons are worthwhile. The Michigan and Florida populations inhabit lakes that differ in temperature regime, food level, and predator abundance (Wyngaard *et al.,* 1982; Elmore, 1983; Wyngaard, 1986). The relative contributions of maturation time, body size, and clutch size to fitness in each population may be related to these differences between the lakes. Confounding selection pressures may have molded these life histories

and contributed to obscuring any relationships that might exist among environmental variables and genetic variances. Nevertheless, a plausible and testable scenario can be constructed that might explain, in part, the observed trends.

One possible explanation is that chronically low food levels in the Michigan lake place a premium on reaching a certain minimum body size, maximizing energy demands of growth and maturation. Small clutches may be the result of a tradeoff between clutch size and egg size, favoring a few large young and enhanced survival in a low food environment. In contrast, rapid maturation and large clutches may be favored in the Florida population, in which predation is intense and mortality falls heaviest upon juveniles (Charlesworth, 1980; Wyngaard *et al.,* 1982). The low additive genetic variances in maturation time and clutch size are consistent with this line of reasoning. At least, they suggest different potentials to respond to selection in the near future of microevolutionary time. Alternatively, low levels of additive genetic variance can result from random drift and founder effects. This latter explanation seems less likely, as plankton population sizes are typically large, *M. edax* is presumed to be highly vagile, and only small amounts of migration are necessary to overcome the effects of random drift.

High levels of additive genetic variance pose problems of interpretation because they can be attributed to a greater variety of causes: weak selection, no selection, changing selection, negative pleiotropy, to name a few. Others have compared heritabilities of various traits between populations in search of relationships between additive genetic variance and selection intensity. Berven and Gill (1983) argued that differences in heritabilities of larval duration and size at metamorphosis among three woodfrog populations suggested that selection intensities were very different in these populations. Arnold (1981) found similar heritabilities of feeding behavior in two geographically isolated snake populations.

The trends exhibited by maternal effects and/or non-additive genetic effects in this study are troublesome but not unusual. The lower dam relative to the sire components of MD female maturation time and FT female body size in the present study may reflect non-random mating among parents with respect to genotype. If sires were mated with dams of similar genotype for a quantitative trait, then the genetic variance contributed by the dam would be masked in a nested design such as that used in this study. The results for *M. edax* probably represent a conservative estimate of the extent to which dominance and maternal effects are present in these traits.

Perhaps the most important issue is whether the level of additive genetic variance reflects the potential response of the population to selection. The moderate and high heritabilities of female and male, respectively, temperature tolerance in the estuarine copepod *Eurytemora affinis* provided an opportunity to determine whether such heritable variation was available to be acted upon by selection. Ketzner and Bradley (1982) exposed *E. affinis* to three different constant temperature regimes and to three variable temperature regimes over a two year period (20–70 generations) and demonstrated genetic divergence among the regimes as well as a decline in the additive genetic variance in one of the selected lines (Bradley and Ketzner, 1982). Other studies using selection experiments to address this question include Istock *et al.* (1975), Dingle *et al.* (1977), Doyle (1978), and Doyle and Hunte (1981). This growing body of empirical studies (review in Dingle and Hegmann, 1982) reveals considerable additive genetic variance to be present in natural populations of many species. The present study is consistent with these reports in that some of the life history traits examined here exhibited considerable additive genetic variance. The suggested contrasting patterns of additive genetic variance present in particular traits between the two *M. edax* populations indicate the need for additional studies of heritable variation of life history

traits in natural populations. Explanations of additive genetic variance are complex and will likely require both examination of genetic correlations and very carefully designed selection experiments as discussed by Istock (1982), Lande (1982), Rose (1982) and Lande and Arnold (1983).

ACKNOWLEDGMENTS

LITERATURE CITED

ALLAN, J. D. 1976. Life history patterns in zooplankton. *Am. Nat.* **110**: 165–180.

ALLAN, J. D. 1984. Life history variation in a freshwater copepod: evidence from population crosses. *Evolution* **38**: 280–291.

ARNOLD, S. J. 1981. Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake *Thamnophis elegans*. *Evolution* **35**: 489–509.

BERVEN, K. A., AND D. E. GILL. 1983. Interpreting geographic variation in life history traits. *Am Zool.* **23**: 85–97.

BRADLEY, B. P. 1978. Genetic and physiological adaptation to seasonal temperatures. *Genetics* **90**: 193–205.

BRADLEY, B. P., AND P. A. KETZNER. 1982. Genetic and non-genetic variability in temperature tolerance of the copepod *Eurytemora affinis* ion five temperature regimes. *Biol. Bull.* **162**: 233–245.

CHARLESWORTH, B. 1980. *Evolution in Age-structured Populations.* Cambridge Studies in Mathematical Biology. Cambridge University Press, Cambridge. 300 pp.

COWELL, B. C., C. DYE, AND R. C. ADAMS. 1975. A synoptic study of the limnology of Lake Thonotosassa, Florida. Part I. Effects of primary treated sewage and citrus wastes. *Hydrobiologia* **46**: 301–345.

DINGLE, H., AND J. P. HEGMANN, eds. 1982. *Evolution and Genetics of Life Histories.* Springer-Verlag, New York. 250 pp.

DINGLE, H., C. K. BROWN, AND J. P. HEGMANN. 1977. The nature of genetic variance influencing photoperiodic diapause in a migrant insect, *Oncopeltus fasciatus. Am. Nat.* **111**: 1047–1057.

DOYLE, R. W. 1978. Ecological, physiological and genetic analysis of acute osmotic stress. Pp. 275–287 in *Marine Organisms: Genetics, Ecology and Evolution,* B. Battaglia and J. A. Beardmore, eds. Plenum Press, New York.

DOYLE, R. W., AND W. HUNTE. 1981. Genetic changes in the components "fitness" and yield of a crustacean population in a controlled environment. *J. Exp. Mar. Biol. Ecol.* **52**: 147–156.

ELMORE, J. L. 1983. Factors influencing *Diaptomus* distributions: an experimental study in subtropical Florida. *Limnol. Oceanogr.* **28**: 522–532.

FALCONER, D. S. 1980. *Introduction to Quantitative Genetics.* Longman, New York. 340 pp.

FISHER, R. A. 1958. *The Genetical Theory of Natural Selection,* 3rd ed. Dover, New York. 291 pp.

GIESEL, J. J., P. A. MURPHY, AND M. N. MANLOVE. 1982. An investigation of the effects of temperature on the genetic organization of life history indices in three populations of *Drosophila melanogaster.* Pp. 189–207 in *Evolution and Genetics of Life Histories,* H. Dingle and J. P. Hegmann, eds. Springer-Verlag, New York.

HELWIG, J. J., AND K. A. COUNCIL, eds. 1979. SAS User's Guide, 1979 edition. SAS Institute, Inc., Cary, NC.

HEMMERLE, W. J., AND H. O. HARTLEY. 1973. Computing maximum likelihood estimates for the mixed A.O.V. model using the W transformation. *Technometrics* **15**: 819–831.

ISTOCK, A. 1982. Some theoretical considerations concerning life history evolution. Pp. 7–20 in *Evolution and Genetics of Life Histories,* H. Dingle and J. P. Hegmann, eds., Springer Verlag, New York.

ISTOCK, C. A. 1981. The extent and consequences of heritable variation for fitness characters. Pp. 61–96 in *Population Biology: Retrospect and Prospects,* Oregon State Colloquium in Biology, C. R. King and P. S. Dawson, eds., Columbia University Press, New York.

ISTOCK, C. A., J. ZISFEIN, AND K. J. VAVRA. 1975. Ecology and evolution of the pitcher-plant mosquito. II. The substructure of fitness. *Evolution* 30: 535–547.

KETZNER, P. A., AND B. P. BRADLEY. 1982. Rate of environmental change and adaptation in the copepod *Eurytemora affinis. Evolution* 36: 298–306.

KERFOOT, W. C., ed. 1980. *Evolution and Ecology of Zooplankton Communities.* Univ. Press New England, Hannover, NH. 793 pp.

LANDE, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63: 607–615.

LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.

LIND, O. T. 1978. Interdepression differences in the hypolimnetic areal relative to oxygen deficits of Douglas Lake, Michigan. *Internationale Vereinigung für Theoretische und Angewandte Limnologie* 20: 2688–2696.

LYNCH, M. 1980. The evolution of cladoceran life histories. *Q. Rev. Biol.* 55: 23–42.

McLAREN, I. A. 1976. Inheritance of demographic and production parameters in the marine copepod *Eurytemora herdmani. Biol. Bull.* 151: 200–213.

ROSE, M. R. 1984. Genetic covariation in *Drosophila* life history: untangling the data. *Am. Nat.* 123: 565–569.

ROSE, M. R. 1982. Antagonistic pleiotropy, dominance, and genetic variation. *Heredity* 48: 63–78.

SEARLE, S. P. 1970. Large sample variances of maximum likelihood estimators of variance components using unbalanced data. *Biometrics* 26: 505–524.

SWALLOW, W. H., AND J. F. MONAHAN. 1984. Monte Carlo comparison of ANOVA, MIVQUE, REML and ML estimators of variance components. *Technometrics* 26: 47–57.

TANTAWY, A. O. 1961. Effects of temperature on productivity and genetic variance of body size in populations of *Drosophila pseudoobscura. Genetics* 16: 227–238.

TUCKER, A. 1957. The relation of phytoplankton periodicity to the nature of the physico-chemical environment with special reference to phosphorus. Morphometrical, physical and chemical conditions. *Am. Midl. Nat.* 57: 300–370.

WELCH, P. S. 1927. Limnological investigations on northern Michigan lakes. I. Physical-chemical studies on Douglas Lake, *Pap. Mich. Acad. Sci. Arts Lett.* 8: 421–451.

WYNGAARD, G. A. 1983. An experimental analysis of the genetic basis of life history variation in *Mesocyclops edax* (Crustacea: Copepoda). Ph.D. Diss., University of Maryland. 94 pp.

WYNGAARD, G. A. 1986. Genetic differentiation of life history traits in populations of *Mesocyclops edax* (Crustacea: Copepoda). *Biol. Bull.* 170: 279–295.

WYNGAARD, G. A., J. L. ELMORE, AND B. C. COWELL. 1982. Dynamics of a subtropical copepod population, with emphasis on the copepod *Mesocyclops edax. Hydrobiologia* 89: 36–48.

WYNGAARD, G. A., AND C. C. CHINNAPPA. 1982. General biology and cytology of cyclopoids. Pp. 485–533 in *Developmental Biology of Freshwater Invertebrates,* R. W. Harrison and R. C. Cowden, eds. Alan R. Liss, Inc., New York.